

Records of *Nebalia* (Crustacea Leptostraca) from the Southern Hemisphere—a critical review

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SYNOPSIS. The species concept '*Nebalia longicornis*' is composed of at least ten distinct species. Besides *N. longicornis* itself four of these were examined and are described in this paper as new species, viz. *Nebalia patagonica* (Magellan region), *N. antarctica* (Antarctic region), *N. falklandensis* (Falkland Islands), and *N. cannoni* (S. Georgia). Other specimens assigned to *N. longicornis* could not be located and have not been described in sufficient detail to elucidate their true identity. This taxonomic confusion originates, in part, from Thiele's (1904, 1905) erroneous interpretation of *N. longicornis* Thomson, 1879 (which Thiele based upon a juvenile of *Sarsinebalia*) and also the excessively wide species concept previously applied to *Nebalia* species.

INTRODUCTION

The first species of *Nebalia* described from the Southern Hemisphere was *N. longicornis* G. M. Thomson (1879). The description was based upon a single mature male from Otago (Dunedin) Harbour on the East Coast of the South Island of New Zealand. Thomson, when describing this species, appears not to have had access to the paper by Claus (1879) in which sexual dimorphism of *Nebalia* was described. He therefore saw in the greatly elongated flagella of the antennae of this specimen a specific character and not an attribute of sexual maturity. This description of *N. longicornis* is too brief to permit an identification of the species. The drawing of the whole animal contains an error with respect to the articulation of the antennule. Only one feature of taxonomic value can be recognized, viz. the presence of only 1 spine on the anteriodorsal corner of the 4th article of the antennular peduncle. But as will be shown below, this feature is of very restricted value. Nothing is known about the fate of the type (Professor J. B. Jillett, personal communication).

Thiele, in two comprehensive reports on material collected by the German Deep Sea ('Valdivia') Expedition (Thiele 1904) and the German South Polar Expedition (Thiele 1905), produced the first major taxonomic contributions on Leptostraca from the Southern Hemisphere, including the description of the new genus *Nebaliella*. In both papers he also dealt with the genus *Nebalia*.

Claus (1887) previously had studied samples of *Nebalia* from widely different localities, but mainly from the Northern Hemisphere and had introduced a very wide species concept based upon a restricted number of morphological characters, viz. the shape of the compound eye, rostrum and the number of articles in the antennal flagellum. Thiele (l.c.) in dealing with his Southern samples of *Nebalia* accepted this species concept and referred all his specimens to *N. longicornis* Thomson (for details cf. section 3.2). Subsequent writers have followed Thiele, although Calman (1917, 1927) and Cannon (1931) expressed doubts concerning the validity of

this taxonomic approach, and Johnson (1970) found its practical application unacceptable.

Dahl (1985) was able to show that Claus' species concept of *Nebalia* was too generalized and that the cosmopolitan *Nebalia bipes* of the western European coast is composed of a number of distinct species having distribution patterns similar to the other benthic invertebrates of this region.

The absence of authentic *N. longicornis* material has restricted progress on taxonomic studies of southern hemisphere Nebalids. In this paper arguments are examined which led Thiele to identify his material as *N. longicornis* (section 3). It also critically reviews, as far as has been possible, the synonymy of the southern hemisphere *Nebalia* species. The author has been fortunate in having had access to some of the most important collections previously referred to *N. longicornis* and a re-examination has led to the recognition of a number of new species described in section 5. In some instances, although lack of material or of adequate descriptions or drawings has made specific identification impossible, enough is known to state that these records refer to undescribed species. These cases are summarized in section 6, together with general conclusions.

THE REDISCOVERY OF NEBALIA LONGICORNIS THOMSON 1879

In 1985 Dr. G. C. B. Poore noted that the Sayce Collection in the Museum of Victoria contained a sample labelled '*N. longicornis*', which he sent to me for study. These specimens are of particular interest because their tube contains two labels, one bearing the inscription 'cootypes' and the other stating that the sample was brought from New Zealand by G. M. Thomson, the author of *N. longicornis*.

The designation 'cootypes' cannot be correct, for Thomson (1879) stated explicitly that when making his description he had only the type at his disposal.

Unfortunately the labels in the tube give no information

concerning the locality from where the specimens were collected. Taking into account the wide but generally accepted species concept introduced by Claus (1887) and the very incomplete original description given by Thomson (l.c.) this inevitably could cause doubt concerning the true identity of these specimens.

The type locality of *N. longicornis* is Otago Harbour, New Zealand. Prof. J. B. Jillett (pers. com.) has informed me that in this Harbour 'there appears to be only one *Nebalia* in the local shallow water habitats' and kindly sent to me three samples of *Nebalia* from several localities within that region. A critical comparison of an adult female from one of these samples with a similar example from the 'cootype' material reveals that they are conspecific and that this recent material unquestionably belongs to *N. longicornis*.

Although most material collected by Thomson came from Otago Harbour it is unfortunate that the true origin of the 'cootypes' is unknown. Therefore it is necessary to create a lectotype and paralectotypes for this species and these have been selected from the recent specimens sent to me by Prof. Jillett (see above and also Section 5).

THE INTERPRETATION OF *NEBALIA LONGICORNIS* BY THIELE 1904

The single specimen of *N. longicornis* having been lost and the description being too brief to permit identification, Thiele (1904) attempted to establish the identity of the only New Zealand specimen available to him of what he presumed to be a *Nebalia*, viz. a small specimen from Akaroa Bay near Christchurch on the East Coast of the South Island. Because this specimen was from New Zealand Thiele felt entitled to conclude 'mit ziemlich grossen Sicherheit' that it belonged to *N. longicornis*.

Thiele (l.c.) noted that this specimen lacked dark eye pigment and had a ventral subterminal rostral spine of which he made a drawing (l.c. pl.4, fig. 67). His concept of *N. longicornis* was influenced by a previous observation made on a sample of Leptostraca from Ireland, composed of small specimens with rostral spine and no dark eye pigment, a somewhat larger juvenile without rostral spine and with dark eye pigment, and an adult specimen of *Nebalia*. From this composite sample Thiele concluded that all the specimens in the sample belonged to *Nebalia* and that juveniles leaving the brood pouch lack dark eye pigment and retain a rostral spine that he presumed to be present in the embryo. This was to him a confirmation that the Akaroa Bay specimen was *N. longicornis*. Thiele had however, overlooked observations by Sars (1896) showing that the dark eye pigment in *N. bipes* begins to form in the brood pouch and that neither embryos nor juveniles possess a rostral spine. This was later confirmed by Manton (1934).

The specimen from Akaroa Bay is in the collections of the Zoological Museum of Copenhagen University. It was apparently damaged when collected and is generally in poor condition. I can however, confirm the absence of dark eye pigment. The eyes appear to be discshaped. There is no row of short 3-pronged spines on the margin of the exopod of the 1st pleopod as diagnostic of the genus *Nebalia* (Cf. SEM micrograph, Dahl 1985 fig. 115). The combination of disc-shaped eyes without dark pigment, a ventral subterminal

rostral spine, and the absence of the spine-row mentioned above is diagnostic of the new genus *Sarsinebalia* (Dahl l.c.). The genus appears to be cosmopolitan and the type of the genus, *S. typhlops* (G.O. Sars 1896) occurs in Irish waters. The Irish sample seen by Thiele (l.c.) obviously contained specimens of both *Nebalia* and *Sarsinebalia*.

The small specimen from Akaroa Bay is not in good enough condition to serve as a basis for a descriptive account, but it is clearly a *Sarsinebalia*. With the exception of a specimen of *Nebaliella antarctica* Thiele (1904), also from the Akaroa Harbour, this was the only leptostracan recorded by Thiele (1904) from New Zealand. As will be shown in section 4 all other samples referred by Thiele (1904, 1905, 1907) to *N. longicornis* belong to other species. Only in one case is this conclusion based on indirect evidence.

It must be concluded, therefore, that Thiele (l.c.) never saw authentic specimens of *N. longicornis*, and his comprehensive discussions concerning the morphology and geographical distribution of this species and his comparisons with *N. bipes* are no longer valid and need not be taken into account.

RECORDS OF THE GENUS *NEBALIA* FROM THE SOUTHERN HEMISPHERE

Claus (1887)

Claus (1887) gave certain information concerning specimens of *Nebalia* from Chile in the Zoological Museum of the University of Vienna, collected by Schmarda. No mention was made of the exact locality. In an ovigerous female 11 mm in length Claus noted 16 articles in the flagellum of the antennule and 17 in that of the antenna. A smaller specimen showed a lower number of articles. The eye-stalk was strikingly long and the ommatidial part covered nearly the whole of it.

Thiele (1904), who had also seen these specimens but had not been permitted to dissect them, referred them, on account of the long rostrum and the armature of the antennule, to the 'Formenkreis der *N. bipes*'.

Claus (l.c.) who had studied specimens of *Nebalia* from different parts of the world concluded (l.c. p. 126) that the Arctic, Atlantic, Mediterranean and Adriatic populations, including what is now *Sarsinebalia typhlops*, belonged to one species which he called *N. serrata*, a name which, if valid, should rightly have been *N. bipes* (O. Fabricius 1780). In a footnote (l.c. p. 127) he named the Chilean form *N. chilensis* but stated that he could not decide whether it should be regarded as a 'Geographische Rasse' of *N. serrata* or as a separate species. Apart from the characters quoted above no description was given, and *N. chilensis*, although most probably referring to a new species, must remain a *nomen nudum*. No information on the specimens could be obtained from Vienna.

Claus (l.c.) also briefly discussed *N. longicornis*. Noting the lack of detail he concluded that his sample from Chile and *N. longicornis* should be regarded as belonging to 'dem engeren Typus aller von mir untersuchten *Nebalia*formen'. This hardly implies more than that both belong to the genus *Nebalia*.

Thiele (1904, 1905, 1907)

Thiele accepted the views held by Claus concerning the extremely wide geographical range of *Nebalia* species and the considerable intraspecific variation. He regarded all specimens of *Nebalia* with a comparatively short and broad rostrum and a single spine on the 4th article of the antennular peduncle as belonging to *N. longicornis* and noted that it was difficult to find other good specific characters. As a result he reported *N. longicornis* from a number of widely separated localities, viz:

Pacific, New Britain, Blanche Bay (*N. longicornis*) (Thiele 1904) Pacific, Loyalty Islands, Lifu, Sandal Bay (*N. longicornis*) (Thiele 1904), Caribbean, Cuba (*N. longicornis soror* ssp. n.) (Thiele 1904), South America, Magellan Region, Ushuaia and Punta Arenas (*N. longicornis magellanica* ssp. n.) (Thiele 1904).

Antarctic, 'Gauss' Winter Station 1902–1903, 66°2'22" S, 89°38' E, 380–385 m (*N. longicornis magellanica*) (Thiele 1905).

This indicates a range of *N. longicornis* from tropical to sub-zero temperatures in the Antarctic and extending into most of the Southern Hemisphere.

According to Thiele (1904) the alleged *N. longicornis* specimens from New Britain and the Loyalty Islands were originally identified by Stebbing as belonging to *N. bipes*. They are not in the British Museum (Natural History) collections, and I have not been able to trace their whereabouts.

The drawing by Thiele (l.c. fig. 66) of the rostrum of a specimen from Blanche Bay, New Britain, is clearly different from that of the selected lectotype specimen of *N. longicornis*. He also figures the compound eye (l.c. fig. 69) without the well-developed eye papilla, clearly present in *N. longicornis*. Thiele's figures undoubtedly represent a new species, but in the absence of material it must remain undescribed.

The sample from Lifu in the Loyalty Islands is without documentation. Our present knowledge of the range of *Nebalia* species suggests that this tropical form is not identical with *N. longicornis* from the cool temperate waters of SE New Zealand.

The specimens from Cuba examined by Thiele (1904) had a comparatively long eye-stalk without a distinct eye papilla (l.c. fig. 77). This is certainly an undescribed species. The sample examined by Thiele belonged to the Zoological Museum, Berlin. The locality is outside the geographical range of the present study material, and I have not found it necessary to examine the specimens.

The new South-American subspecies *N. longicornis magellanicus* Thiele (1904) was probably based upon specimens from Punta Arenas on the Straits of Magellan collected by Ohlin (1896). Ohlin (1901) reports that he first identified this species as *N. longicornis*, but after comparisons with Arctic specimens of *N. bipes* he concluded that the two species were identical. Thiele (l.c.) based his identification of *N. longicornis* upon the presence of only 1 spine on the 4th article of the antennular peduncle and he regarded the well-developed eye papilla as diagnostic of the new subspecies *N. l. magellanica* (l.c. fig. 68). Thiele (1905) mentioned further specimens from the Magellan region obtained by German collectors at Ushuaia and Punta Arenas in depths of 0–20 m, from which he confirmed the original observations on the compound eye.

The collections of the Swedish State Museum of Natural

History examined by myself contain 7 samples of *Nebalia* from the Straits of Magellan and Tierra del Fuego, collected by various Swedish expeditions in the intertidal zone or in shallow water. All these samples contain only one species.

These specimens have the same armature on the antennule and the same characteristic eye papilla as drawn by Thiele for *N. l. magellanica*. Moreover some samples, like those studied by Thiele, come from Punta Arenas and Ushuaia. They are undoubtedly conspecific with those described by Thiele as *N. l. magellanica*. However, a comparison with the lectotype of *N. longicornis* reveals many differences and therefore *N. l. magellanica* must be regarded as a new species. It is permissible to use the subspecific name 'magellanica' for this new species, but unfortunately, as will be shown below, Thiele also referred another well-defined new species to *N. l. magellanica*. To avoid unnecessary confusion the Magellan species is therefore named *N. patagonica* n.sp. and described in section 5.

In his report on the Leptostraca of the German South Polar Expedition Thiele (1905) recorded one sample from the 'Gauss' winter station at 66°22'2" S, 89°38'E, 380–385 m. The sample consisted of 4 specimens, which he referred to the genus *Nebalia*. He noted, however, that the smallest specimen had the same type of rostrum with subterminal ventral spine and the same poorly developed compound eyes typical of his specimen from Akaroa Harbour, New Zealand. This specimen most probably represents another species of Sarsinebalia.

From one of the other three specimens, a large immature male, Thiele (l.c.) made drawings of the rostrum, compound eye, and 4th peduncular article of the antennule. Although aware of the fact that both the shape of rostrum and compound eye of his Antarctic specimens differed from those of his Magellanic material, he regarded the Antarctic ones as belonging to *N. l. magellanica*. Later (Thiele 1907) in his report on the Leptostraca of the British National Antarctic Expedition recorded the occurrence of numerous specimens of *N. l. magellanica* from a number of localities in the Ross Sea, and illustrated some of these. Calman (1917) found that a further specimen from the entrance of McMurdo Sound also agreed perfectly with the drawings made by Thiele. Having seen all the specimens from the Ross Sea and also a specimen from Commonwealth Bay, King George V Land, reported upon by Calman (1918), I share the view expressed by Calman (l.c.) that all these specimens from Antarctic coastal waters, including those from the 'Gauss' winter station, belong to the same species. This is also the case for the samples of *Nebalia* reported by Ledoyer (1969) from various shallow water localities off Adélie Land. The observations recorded by Ledoyer (l.c.) show that his specimens agree with descriptions and drawings made by Thiele (1905, 1907) of the specimens from Wilhelm II Land and Ross Sea and are therefore to be regarded as belonging to the same species. It is therefore now possible to conclude that hitherto only one *Nebalia* species, recorded from Wilhelm II Land, Adélie Land, King George V Land, and the Ross Sea, has been found in the coastal waters of the Antarctic continent.

However, comparisons of this large Antarctic species with *N. longicornis* and *N. patagonica* make it clear that it differs from both in many respects and that it must be designated as a new species. It is described in section 5 under the name *N. antarctica* n.sp.

Calman (1917, 1918)

As noted above, Calman (1917, 1918) contributed materially to the knowledge of *N. antarctica* n.sp., to be described below.

In addition, however, Calman (1917) in his report on the Leptostraca of the British Antarctic 'Terra Nova' Expedition 1910, recorded two specimens of Leptostraca, tow-netted off Northern New Zealand, one at st. 10, in the surface near Three Kings Island and the other at st. 15 in Spirits Bay.

Calman noted that both specimens were immature, one of them possessing a ventral subterminal rostral spine, 'regarded by Thiele as a juvenile character'. Calman provisionally referred both specimens to *N. longicornis*, at the same time however, expressing his doubts concerning the status of the species and the value of the presumed diagnostic characters. I have seen these two specimens which are in the collection of the British Museum (Natural History), but they are both juveniles and hardly suited to form the basis of a taxonomic description and I have refrained from dissecting them. The one with a small rostral spine is certainly a *Sarsinebalia*, the other one a *Nebalia*.

Cannon (1931)

Cannon (1931) reported upon the Leptostraca of the 'Discovery' collection. He dealt, in the first place, with *Nebaliopsis typica* G.O. Sars and *Nebaliella extrema* Thiele but also briefly with some samples of *Nebalia* and commented, like Calman (1917, 1927) upon the unsatisfactory status of *Nebalia* taxonomy.

I have been able to study this 'Discovery' material. It contains 4 samples of *Nebalia*, listed below together with the tentative identifications made by Cannon (l.c.) for three of them.

South Georgia, st. 45. 2.7 miles S. Jason Light. 6.IV.1926, 238–270 m, *N. longicornis magellanica*.

South Georgia, St. 144. 54°04'—53°58' S, 36°27'—36°26' W. 4.V.1926. 157–178 m Not mentioned by Cannon.

Falkland Islands, st. 51 off Eddystone Rock. 4.V.1926. *N. l. magellanica*.

South Africa, Simonstown, False Bay, Basin of H. M. Dockyard, 11.VIII.1926, 1–2 m. *N. longicornis*.

None of these specimens belong to *N. longicornis*. This is not surprising considering the vast distances separating the respective 'Discovery' stations from the type locality in New Zealand.

The two samples from S. Georgia both represent a new species, described in section 5 as *N. cannoni* n. sp. The single specimen from the Falkland Islands it also a new species, described in section 5 under the name *N. falklandensis* n. sp.

The specimen from Simonstown, S. Africa belongs to *N. capensis* K. H. Barnard (1914).

Other records

Reference has already been made above to the paper by Ledoyer (1969), which contributes information on *N. antarctica* n.sp.

Wakabara (1965) recorded and discussed a species of *Nebalia* collected in Brazil at Ubatuba, 23°57'S, 45°06'W. His drawings show considerable individual variation of the spinous armature of the 4th article of the antennular peduncle in his 6

male and female specimens. A reference to the lack of denticulation is difficult to understand. If it refers to pleopods 3 and 4 it is worth noting. This is undoubtedly a new species which should be given a complete description.

Johnson (1970) reported the presence of a population of *Nebalia* at Singapore. He discussed critically the specific criteria applied by Claus (1887) and Thiele (1904, 1905, 1907) and, finding them unsatisfactory, did not specifically identify his specimens.

From Southern Africa two valid species have been described, viz. *N. capensis* K. H. Barnard (1914) from Cape Town (cf. above) and *N. ilheoensis* Kensley (1976) from S. W. Africa.

Finally Dahl (1985) reported *N. strausi* Risso from St. Helena. The species is also known from Madeira, the Western Mediterranean and the West Coast of Europe to NW France and the Channel Islands.

DESCRIPTIONS

Nebalia longicornis Thomson (1879).

Description of female lectotype.

TYPE LOCALITY: New Zealand, South Island, Otago Harbour, Portobello Mar. Biol. Stat. Locality 14 B 12₂, 18 fathoms. July 7, 1965. 2 paralectotypes.

Status of female: Postovigerous.

Carapace length: 2.7 mm.

Rostrum: long and narrow (fig. 1), 2.6 times as long as wide, slightly broader near base, tapering very gradually to comparatively narrow, rounded point.

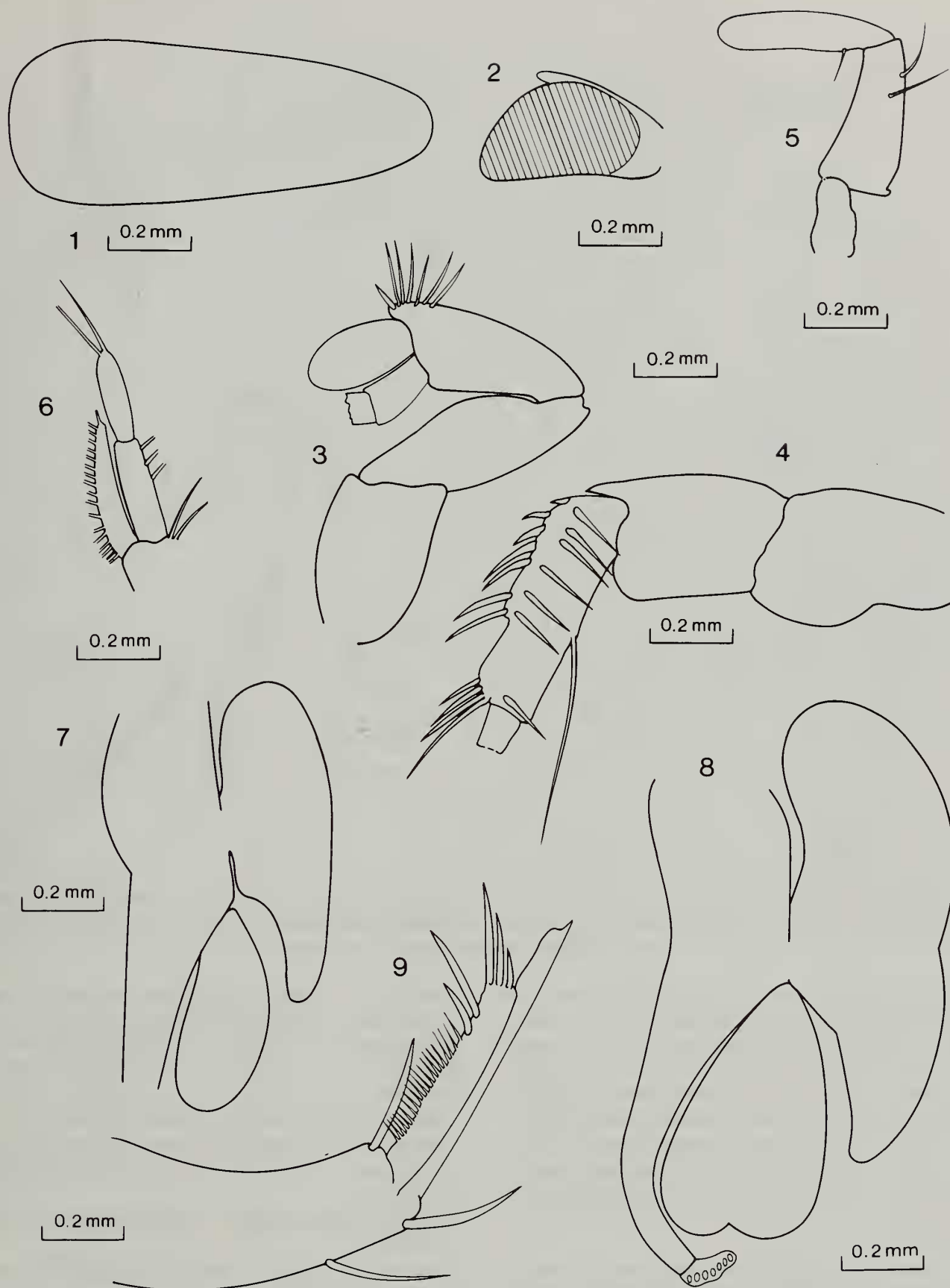
Pleon, telson, furca: 4th pleon epimeron (fig. 10) with posterolateral corner produced to form acute point, posterior margin with comparatively long, rounded denticles, becoming gradually somewhat broader proximally. Crenulation on dorsum of pleon segments 6 and 7 (fig. 14) with denticles rather long, distally rounded and not very closely packed. Anal scales (fig. 15) with medial margin slightly convex, point long and acute over medial part of scale, lateral margin very slightly concave, sloping evenly and lacking 'shoulder'. Furcal rami (fig. 16) shorter than combined length of telson and 7th pleon segment, only proximal part of medial margin with setae between lateral spines, lateral margin only with dense row of spines.

Compound eye: (Fig. 2) with well developed eye papilla produced over dorsum of eye, ommatidial part covering most of the eye-stalk. Supraorbital plate over both compound eyes damaged.

Antennule: (fig. 3) with 2nd article of peduncle somewhat longer than 3rd article; 4th article with only one spine on distal corner and 6 setae along dorsal margin. Antennular scale elliptic, 2 times as long as wide. Flagellum of both antennules broken near base.

Antenna: (fig. 4) with peduncular articles comparatively short; 3rd article only slightly longer than 2nd article, on right antenna with lateral spine-row composed of 8 spines plus one distal spine, on left antenna only 6 spines, some possibly lost.

Mandibular palp: (fig. 5) with 2nd and 3rd articles subequal in length; 2nd article with one small tubercle on proximal corner and one marginal and one lateral seta on distal part, both rather short; 3rd article straight, only expanding very slightly



Figs 1-9 *Nebalia longicornis* G. M. Thomson, female lectotype. 1. Rostrum. 2. Compound eye. 3. Antennule. 4. Antenna. 5. Mandibular palp. 6. Maxillary palp. 7. 1st thoracopod. 8. 3rd thoracopod. 9. 1st pleopod.

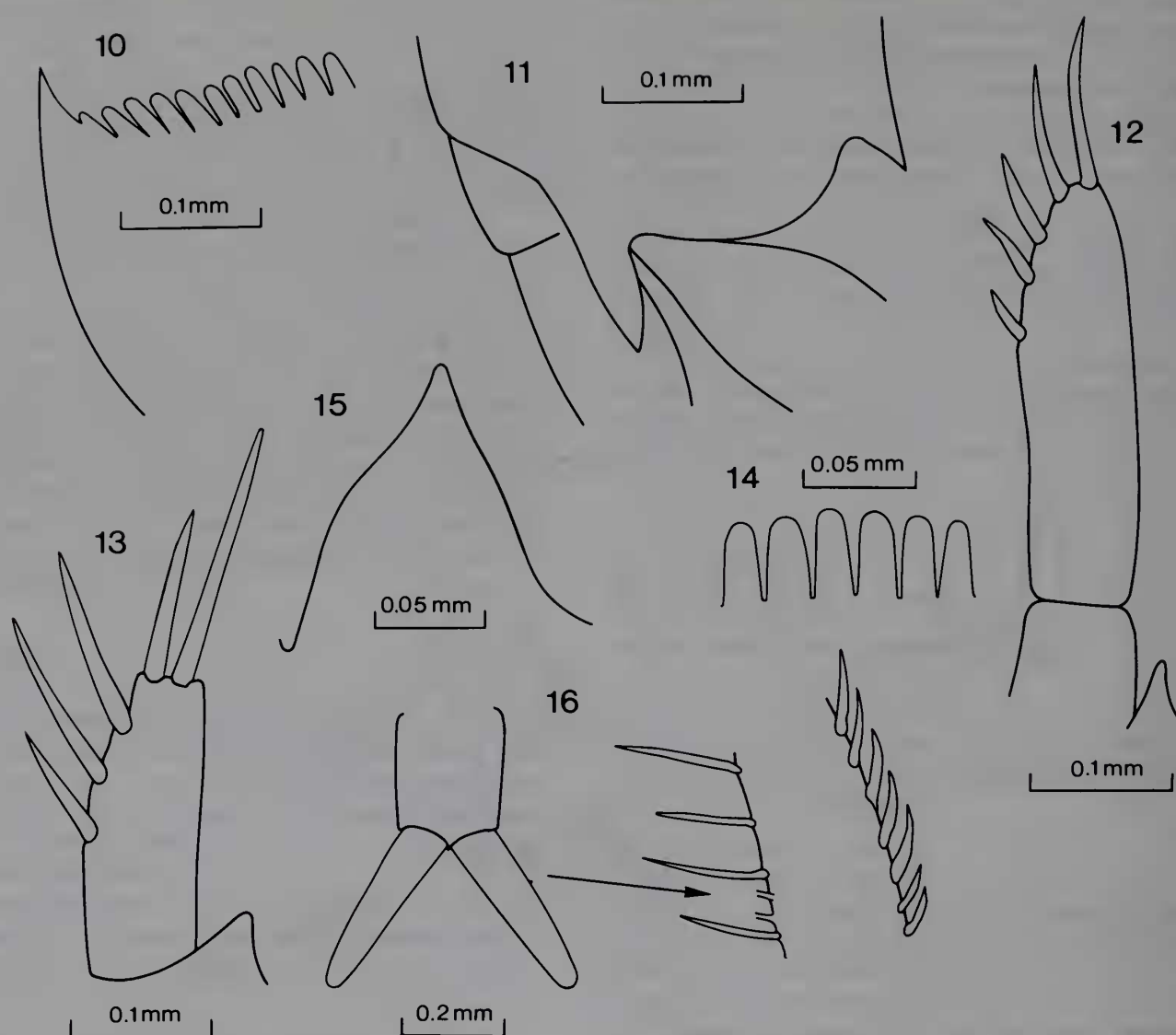
distally. Of marginal spine-row only position of proximal spine indicated in fig. 5. Proximal 8 spines in marginal row shorter than the distal ones, the 9th spine intermediary.

2nd maxilla: (fig. 6) with distal article of palp of endopod only slightly shorter than proximal article. Exopod reaching past end of 1st article of endopod.

Thoracopods: Endopod of both 1st thoracopods broken distally (fig. 7). Exopod narrow, only as broad as basal part of

endopod, epipod reaching to middle of exopod, 3rd thoracopod (fig. 8) with broad exopod, exopod reaching past middle of endopod.

Pleopods: Endopod of 1st pleopod only slightly shorter than peduncle. Terminal posterior spine on peduncle reaching past middle of row of marginal spines on exopod which is composed of about 22 spines. Distal to the spine-row there are 2 subterminal and 3 terminal spines (fig. 9); 4th pleopod



Figs 10—16 *Nebalia longicornis* G. M. Thomson, female lectotype. 10. 4th pleon segment epimeron. 11. 4th pleopod, distal part of peduncle and bases of endopod and exopod. 12. 5th pleopod. 13. 6th pleopod. 14. Crenulation on posterior dorsal margin of 7th pleon segment. 15. Anal scale. 16. Furcal rami with detail of armature.

(fig. 11) with posterolateral corner of peduncle produced and acutely pointed. Process in front of exopod attachment blade-shaped; 5th pleopod (fig. 12) with process between bases of rami short, narrowly triangular and with point sub-acute; 2nd article more than 3 times as long as wide, with 3 spines on distal third of lateral margin and 2 terminal spines (fig. 12); 6th pleopod (fig. 13) with process between rami forming a like-sided triangle, point sub-acute. Rami less than 3 times as long as wide, with 3 spines on distal half of lateral margin and 2 terminal spines.

COMPARISON between lectotype and postovigerous female, carapace length 2.4 mm, from sample in Museum of Victoria, locality unknown, brought from New Zealand by Mr. G. M. Thomson and labelled 'cootypes', specimen referred to below as 'Thomson specimen'.

Rostrum: (figs. 1 and 17), general shape identical, greatest length/width ratio in both cases 2.6.

4th pleon epimeron: (figs. 10 and 26), identical.

Crenulation: on pleon segments 6 and 7 (figs. 14 and 29), identical.

Anal scales: (figs. 15 and 30), nearly identical.

Furca: (figs. 16 and 31), proportions similar, in lectotype

setae between spines only on proximal part of medial margin, in Thomson specimen along whole margin.

Compound eyes: (figs. 2 and 18). General shape, eye papilla, and extension of ommatidial part practically identical.

Antennule: (figs. 3 and 19), closely similar.

Antenna: (figs. 4 and 20), similar but in both specimens minor variations in number of lateral spines on 3rd article of peduncle.

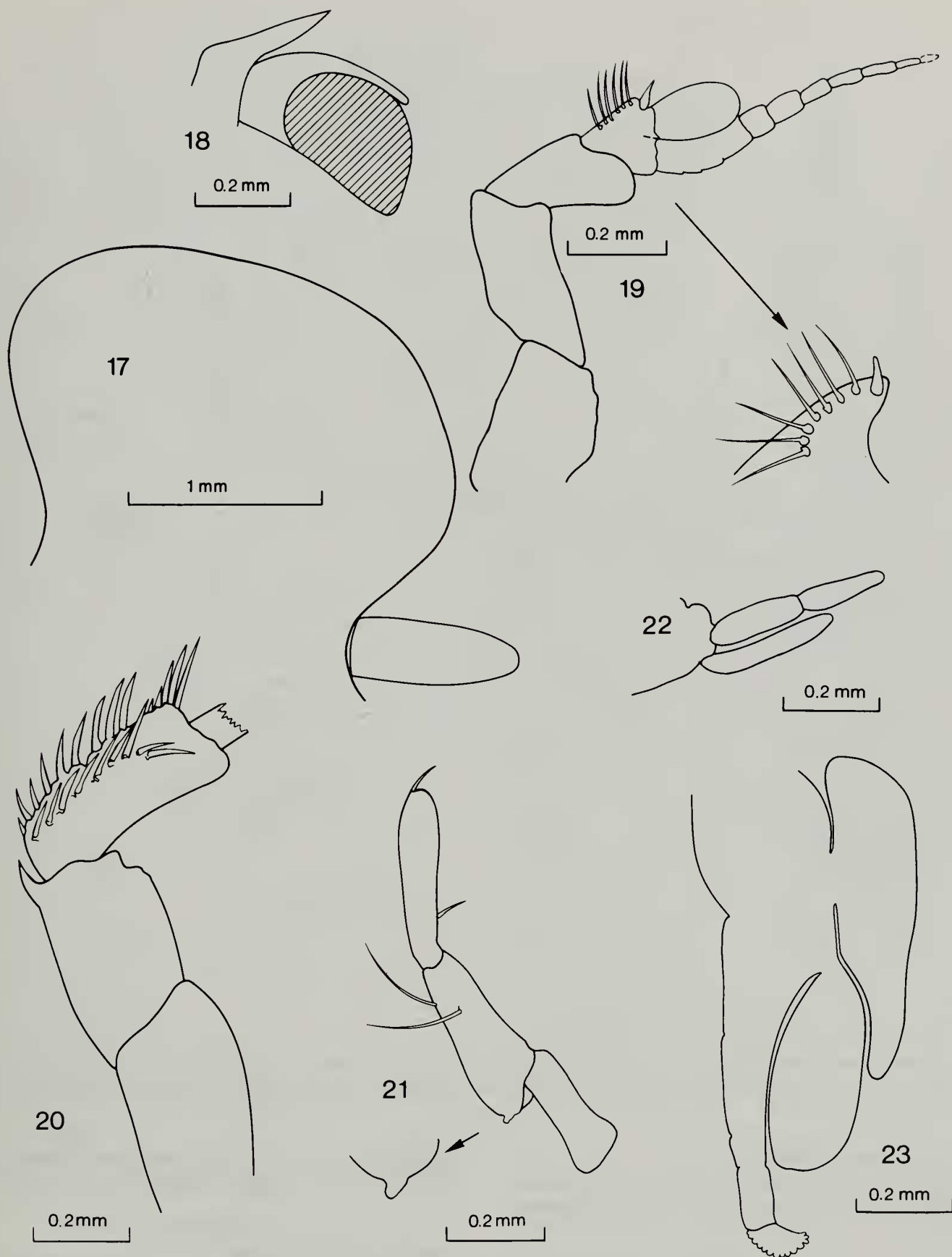
Mandibular palp: (figs. 5 and 21), proportions and armature identical.

2nd maxilla: (figs. 6 and 22), proportions and armature identical.

Thoracopods 1 and 3: (figs. 7, 8 and 23, 24), proportions practically identical.

Pleopods 1 and 4: (figs. 9, 10 and 27, 28), proportions and armature similar, process in front of exopod of pleopod 4 appears slightly more curved in Thomson specimen, which might be due to small differences in perspective.

Pleopods 5 and 6: (figs. 12, 13 and 27, 28), proportions similar, processes between rami identical in shape, but with point more acute in Thomson specimen. Lateral and distal marginal spines totalling 5 in lectotype and 4 in Thomson specimen.

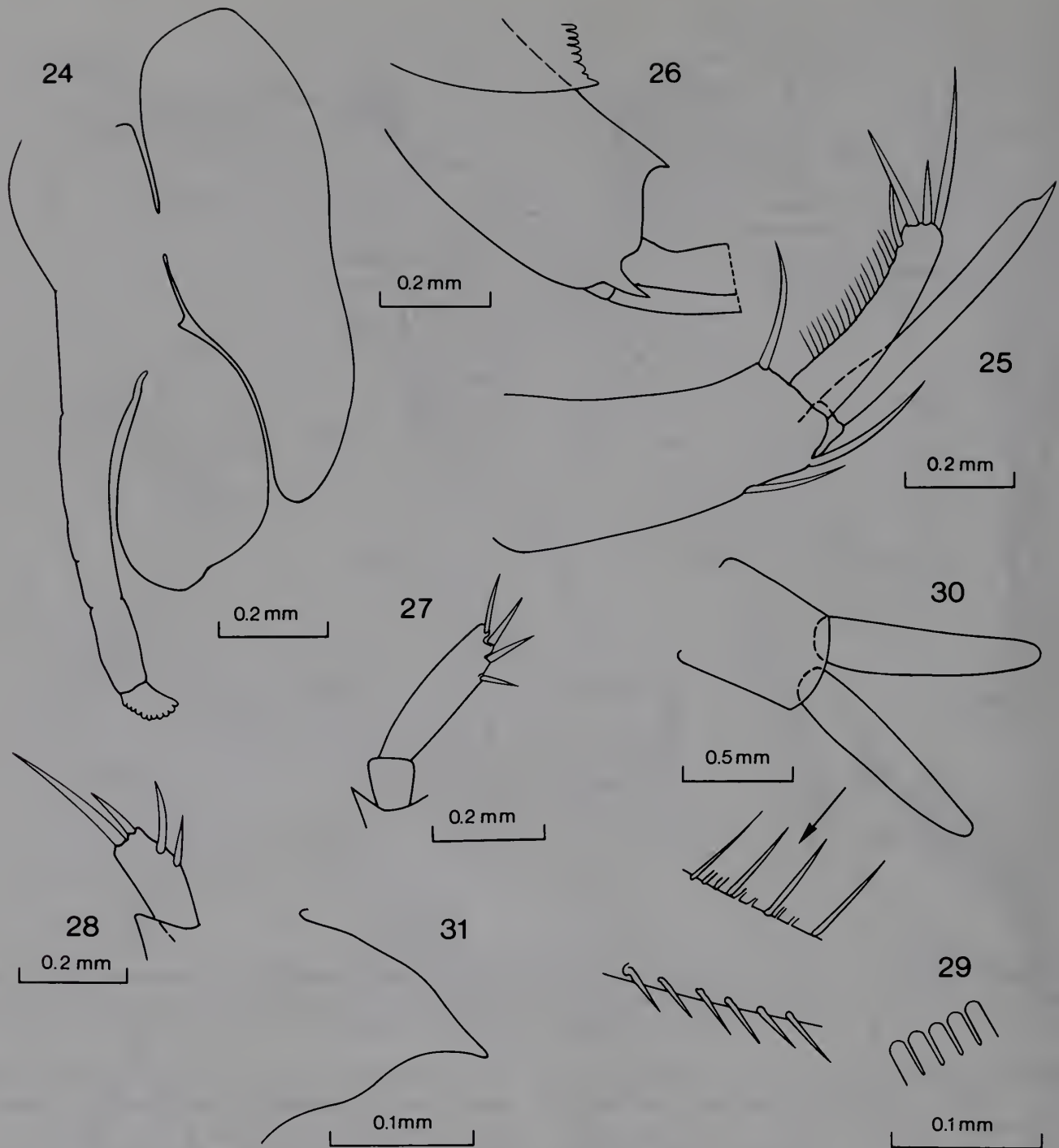


Figs 17–23 *Nebalia longicornis*, 'Thomson specimen'. 17. carapace valve and rostrum. 18. Compound eye. 19. Antennule. 20. Antenna. 21. Mandibular palp. 22. Maxillary palp. 23. 1st thoracopod.

As shown by this comparison the shape and proportion of parts are practically identical in both specimens. Minor differences in armature were observed, but such individual and growth related variations occur regularly in *Nebalia* (Dahl 1985).

The close similarity with respect to all morphological characters confirms that the lectotype and the Thomson specimen belong to the same species. The lectotype comes

from Otago Harbour, where Thomson collected his original single specimen. The fact that Thomson made most of his collecting there makes it highly probable, although not possible to prove, that his 'cootypes' came from the same area. It is reasonable to conclude that the identity of *Nebalia longicornis* Thomson is now definitely established. The lectotype and paralectotypes of *N. longicornis* are in the New Zealand National Museum, Wellington.



Figs 24—31 *Nebalia longicornis*, 'Thomson specimen'. 24. 3rd thoracopod. 25. 1st pleopod. 26. 4th pleon segment epimeron and proximal part of 4th pleopod. 27. 5th pleopod. 28. 6th pleopod. 29. Crenelation on posterior margin of 7th pleon segment. 30. Telson and furca. 31. Anal scale.

ADDITIONAL MATERIAL EXAMINED

1. New Zealand, Otago Harbour, Portobello Marine Laboratory, locality B 7 (1) 6 fathoms, June 17, 1965, 1 specimen.
2. Same area, Loc. B 10₂, 6 fathoms, June 6, 1965, 1 specimen.

Nebalia patagonica n. sp.

Description of female holotype.

NOTE. The material of *N. patagonica* is not in a perfect condition. The 2nd maxilla and the thoracopods could not be separated in any of the specimens and are therefore not included in the description. Other diagnostic features are, however, available and permit a description leaving no doubts concerning the identity of the species.

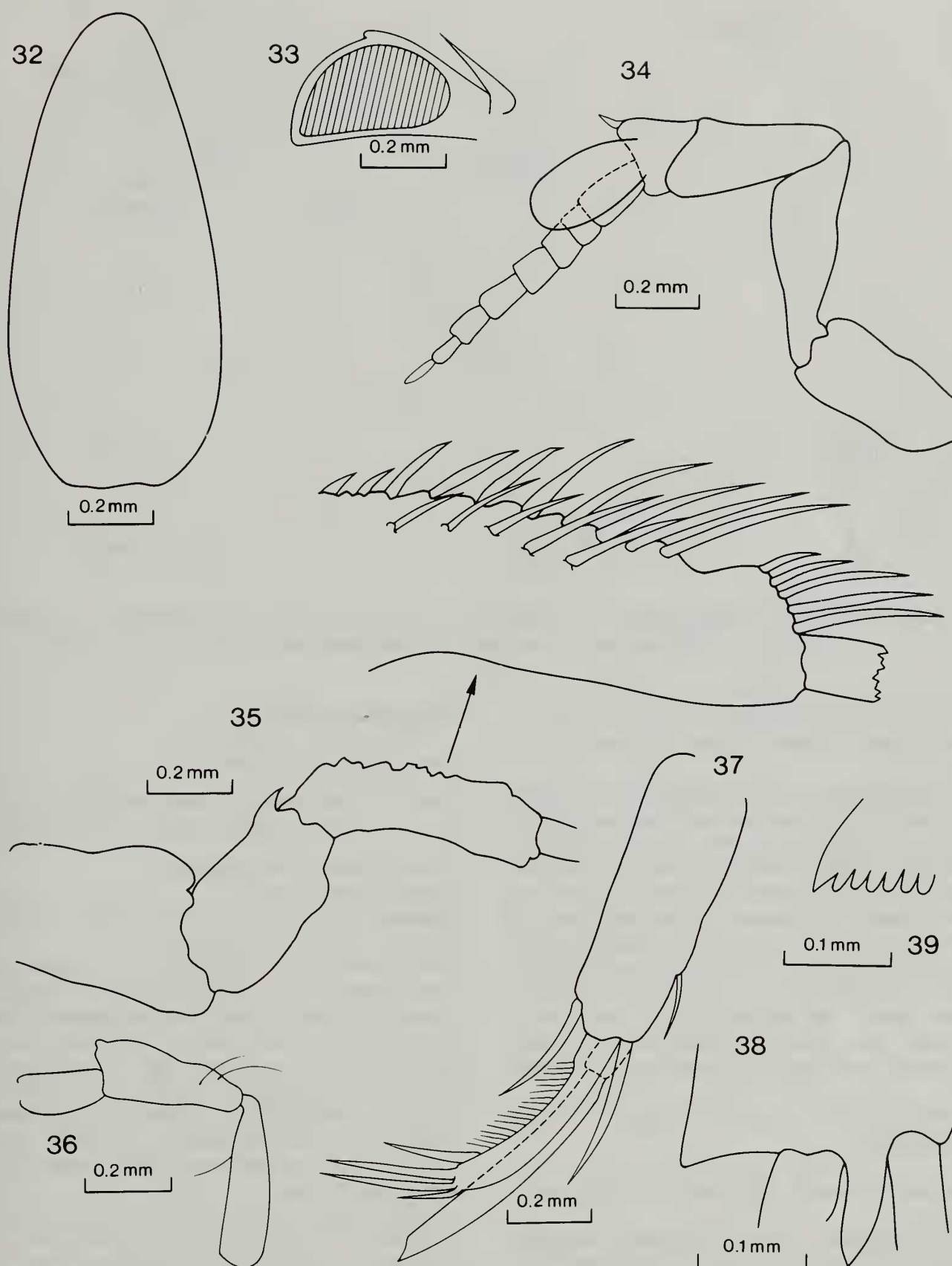
TYPE LOCALITY: Tierra del Fuego, Canal Magdalena, Hope Harbour, 6–10 m, rocks with algae, April 30, 1894.

Status of female: Prae-ovigerous.

Carapace length: 2.5 mm.

Rostrum: (fig. 32) expanding slightly near base and then tapering evenly to a rather narrow, rounded point.

Pleon, telson, furca: Posterolateral corner of 4th pleon epimeron pointed but only slightly produced, denticles along posterior margin rounded (fig. 39). Denticles on posterior margin of pleon segments 6 and 7 tapering very slightly distally but with rounded tips (fig. 42). Anal scales (fig. 43) with medial margin broadly convex, point very short, over centre of scale, 'shoulder' broad and rather distinct. Furcal rami (fig. 44) hardly tapering distally and subequal in length to combined length of pleon segment 7 and telson.



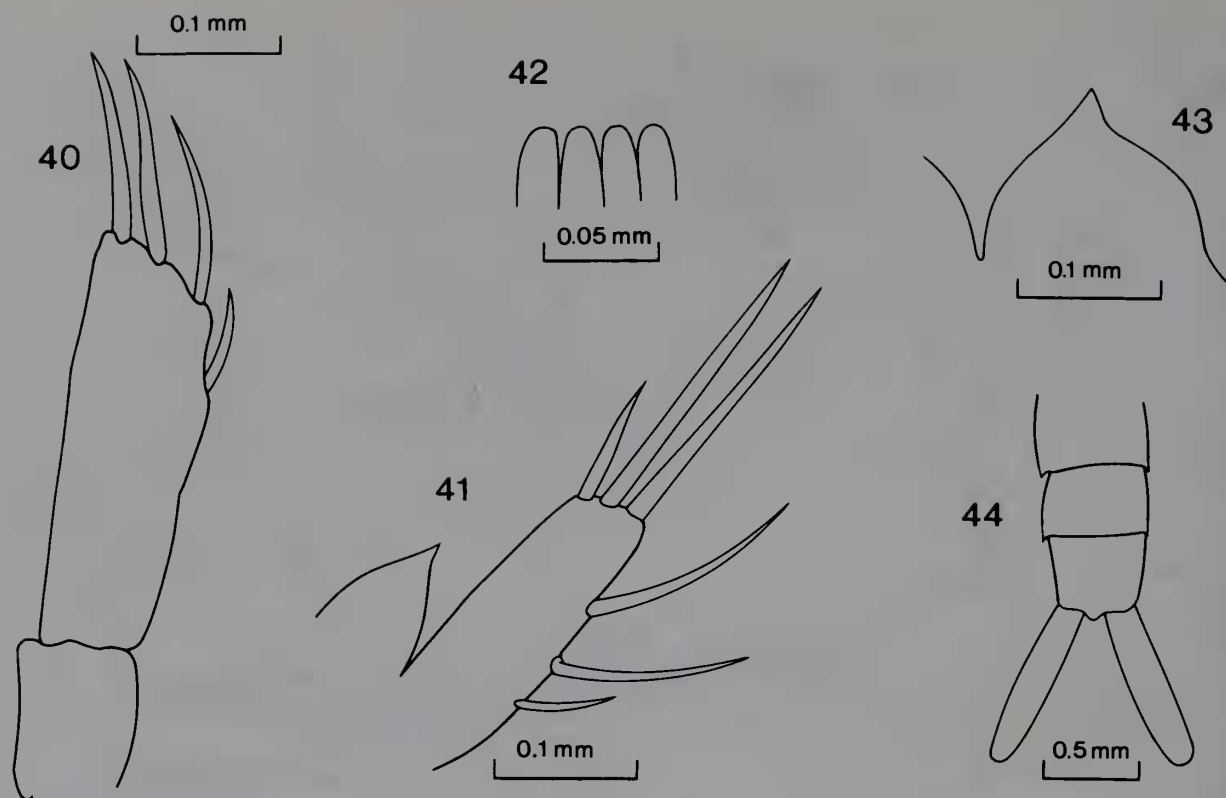
Figs 32—39 *Nebalia patagonica* n. sp., female holotype. 32. Rostrum. 33. Compound eye. 34. Antennule. 35. Antenna. 36. Mandibular palp. 37. 1st pleopod. 38. 4th pleopod. 39. 4th pleon segment epimeron.

Compound eye: (fig. 33) with small but distinct eye papilla. Ommatidial area covering more than $2/3$ of the length of the eye-stalk. Supraorbital plate projecting past proximal ommatidia.

Antennule: (fig. 34) with 2nd article of peduncle slender and distinctly longer than 3rd article; 4th article with only 1 spine on distal dorsal corner. Antennular scale about twice as long as wide. Flagellum much shorter than peduncle, with 7 articles.

Antenna: (fig. 35) with 3rd article of peduncle distinctly longer than 2nd article. Lateral spine-row on 3rd article with fewer spines than marginal row, only 5 present in type.

Mandibular palp: (fig. 36) with 2nd and 3rd articles subequal in length, the 2nd article with small tubercle on proximal corner and one subterminal and one lateral seta, both of medium length; 3rd article distinctly expanded distally,



Figs 40—44 *Nebalia patagonica* n. sp. female holotype. 40. 5th pleopod. 41. 6th pleopod. 42. Crenelation on posterior dorsal margin of 7th pleon segment. 43. Anal scale. 44. Pleon, telson, furca.

lateral spine-row covering the distal 2/3 of the margin (cf. the position of the proximal spine indicated in fig. 36).

Pleopods: 1st pleopod (fig. 37) with lengths of peduncle and endopod subequal. Curved subterminal spine on posterior margin of peduncle reaching to centre of row of 17 short spines on margin of exopod. Distally the exopod carries one subterminal and 3 terminal spines; 4th pleopod (fig. 38) with posterolateral corner of peduncle rectangular and not produced. Process in front of exopod base blade-shaped and nearly straight; 5th pleopod (fig. 40) with 2nd article about 3 times as long as wide and with only 1 lateral, 1 subterminal and 2 terminal spines; 6th pleopod (fig. 41) with ventral process between rami slightly pear-shaped and acutely pointed, 3 lateral spines set well apart and 3 terminal spines.

Holotype and paratypes in the State Museum of Natural History, Stockholm.

FURTHER MATERIAL EXAMINED: All samples come from the Magellan region.

1. Straits of Magellan, Punta Arenas, intertidal, sand under stones. 'Not rare'. 5 specimens. Dec. 2, 1896. Swed. Exp. to Tierra del Fuego.
2. Puerto Churruca, 20 fathoms, dead shells. 1 specimen. March 26, 1896. Swed. Exp. to Tierra del Fuego.
3. Fortescue Bay, 10–12 fathoms, algae. March 25, 1896. 1 specimen. Swed. Exp. to Tierra del Fuego.
4. Beagle Channel, Ushuaia, clay, 10 fathoms. May 5, 1896, 1 specimen. Swed. Exp. to Tierra del Fuego, and 6 m., clay, 1 specimen, Oct. 10, 1902 Swed. Antarct. Exp.

All these samples are in the State Mus. Nat. Hist., Stockholm.

TYPE: no. 3960

Nebalia antarctica n. sp.

Description of female holotype.

TYPE LOCALITY: Antarctic, Ross Sea, 'Discovery' Expedition, W. 2., no 4 hole, 4 fathoms, Jan, 10, 1903. 84 paratypes.

Status of female: Prae-ovigerous.

Carapace length: 5 mm.

Rostrum: (fig. 45). Sides nearly parallel, distally tapering slightly to broadly rounded apex.

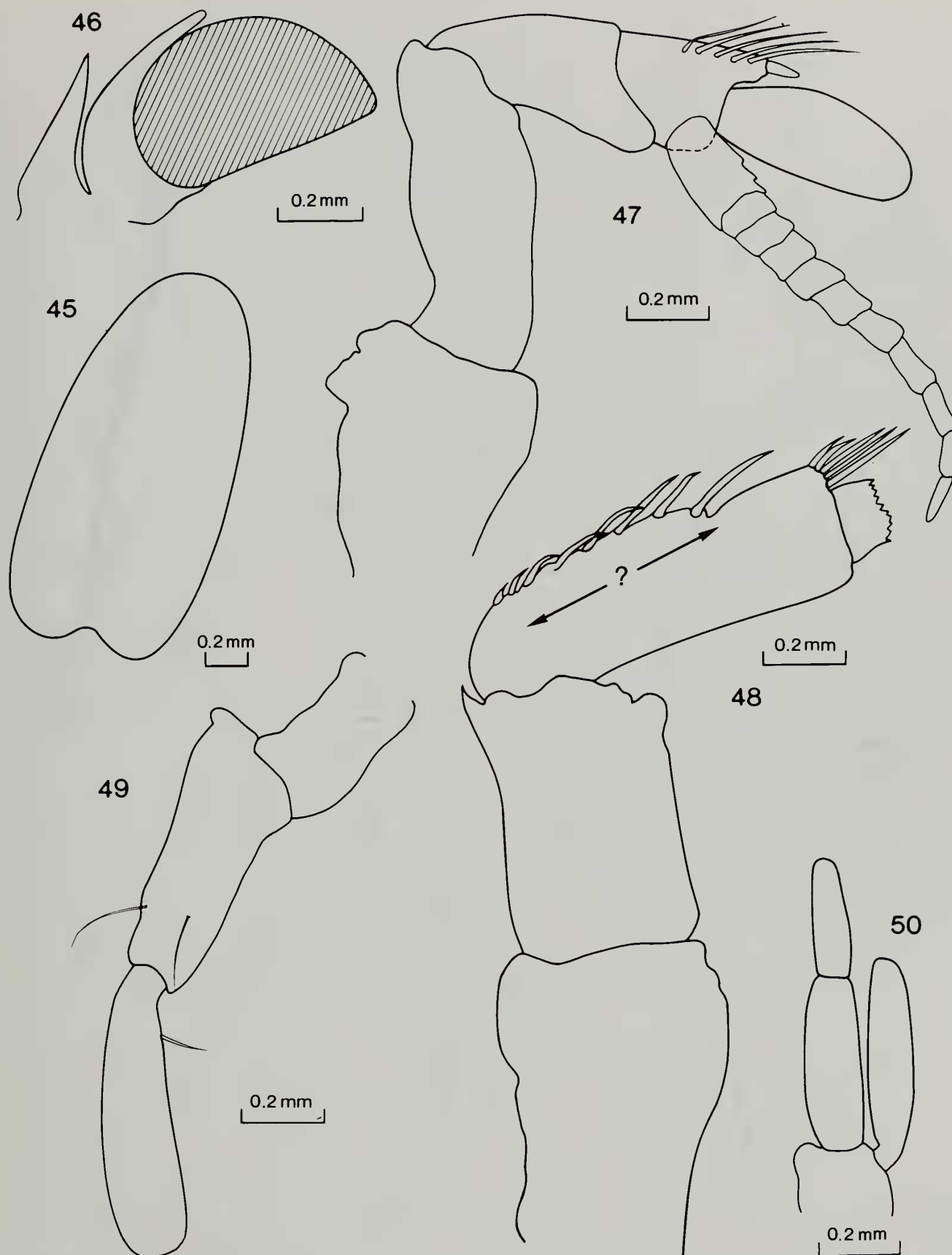
Pleon, telson, furca: Epimeron of 4th pleon segment with posterolateral corner produced and acutely pointed (fig. 56), denticles on posterior margin acutely pointed. Posteriodorsal margins of pleon segments with denticles tapering to acute points (fig. 61). Anal scales (fig. 62) with medial margin slightly concave and with long, acute points over medial part of scale. Lateral margins sloping steeply without distinct 'shoulders'. Furcal rami (fig. 63) tapering very slightly to rounded apices, slightly longer than combined length of 7th segment and telson.

Compound eye: (fig. 46) with ommatidial part covering 2/3 of eye-stalk. Eye papilla strongly developed, distal part produced, projecting freely over dorsum of eye. Supraorbital plate short, just reaching to level of proximal ommatidia.

Antennule: (Fig. 47) with 2nd article longer than 3rd article, 4th article with only 1 spine on distal corner. Antennular scale slightly more than twice as long as wide and with posterior margin nearly straight. Flagellum distinctly shorter than peduncle, with 11 articles.

Antenna: (fig. 48). 3rd article of peduncle rather short, only slightly longer than 2nd article. The details of the lateral spine-row could not be studied.

Mandibular palp: (fig. 49) with 2nd and 3rd articles nearly equal in length, the 3rd article slightly longer; 2nd article with



Figs 45—50 *Nebalia antarctica* n. sp., female holotype. 45 rostrum. 46. Compound eye. 47. Antennule. 48. Antenna. 49. Mandibular palp. 50. Maxillary palp.

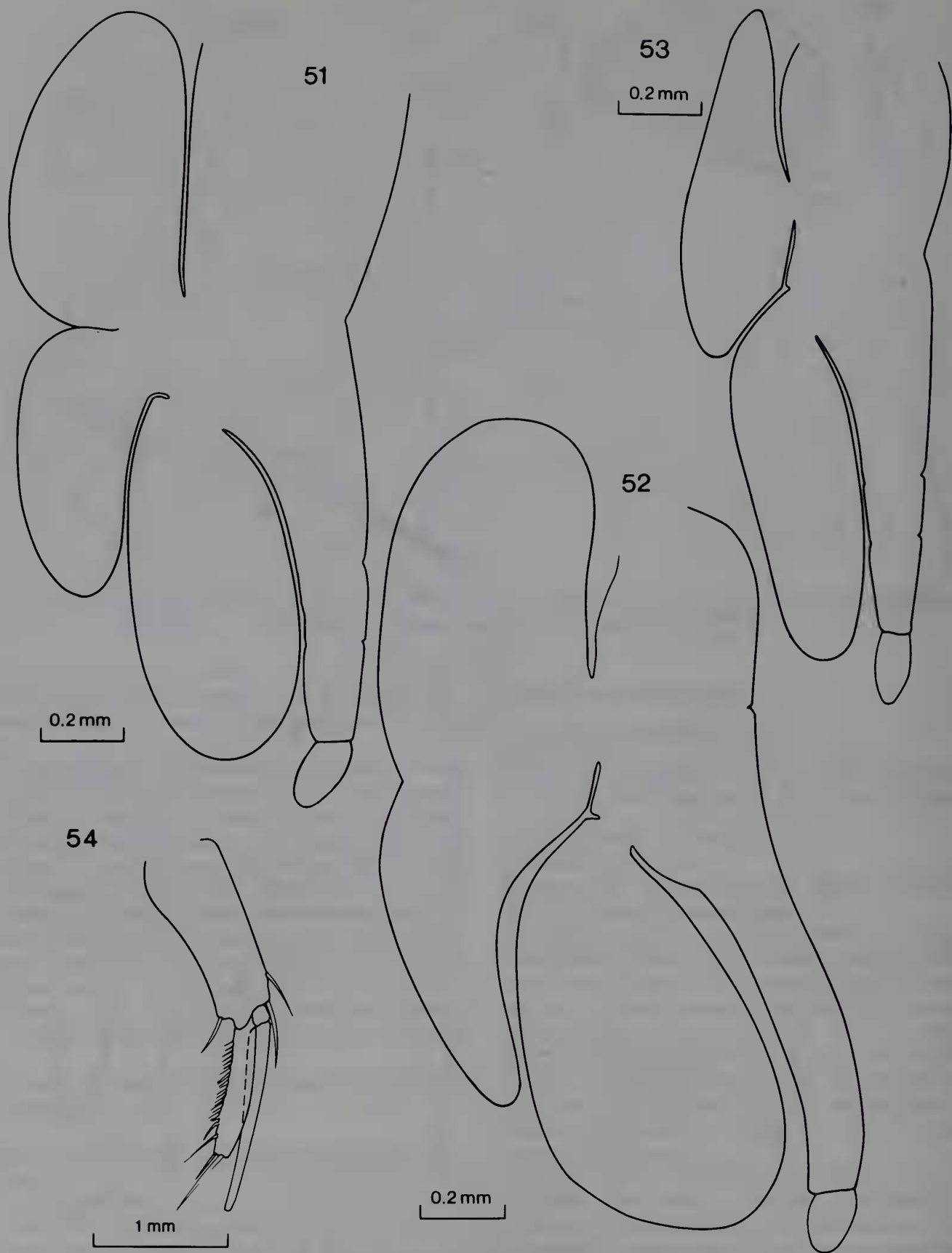
small tubercle on proximal corner. One short subterminal seta on margin and one short lateral seta, 3rd article expanding distally, marginal spine-row along approximately 4/5 of margin (cf. position of proximal spine in fig. 49).

2nd maxilla: (fig. 50), distal article of endopod palp more than 2/3 the length of 1st article, exopod reaching beyond apex of 1st article.

Thoracopods: 1st thoracopod (fig. 51) with exopod reaching

level of base of endopod terminal article, epipod reaching to middle of exopod. Third thoracopod (fig. 52) with broad exopod reaching nearly to end of endopod. Distal lobe of epipod reaching beyond middle of exopod. Eighth thoracopod (fig. 53) with narrow, parallel-sided exopod reaching beyond base of terminal endopod article, epipod with distal lobe very short.

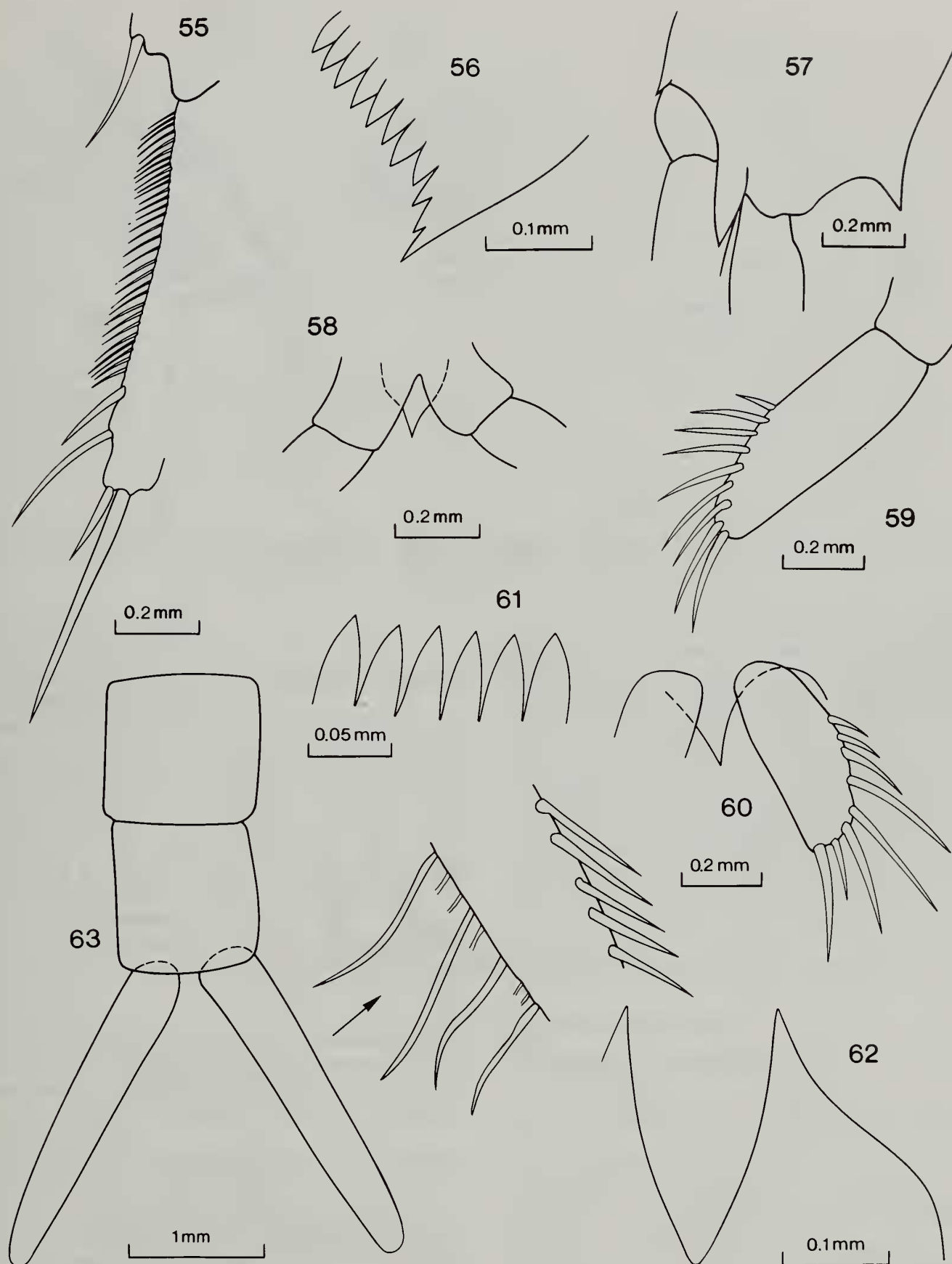
Pleopods: First pleopod (fig. 54) long and slender, endopod



Figs 51—54 *Nebalia antarctica* n. sp., female holotype. 51. 1st thoracopod. 52. 3rd thoracopod. 53. 8th thoracopod. 54. 1st. pleopod.

slightly longer than peduncle, exopod strikingly long, more than $\frac{2}{3}$ the length of endopod. Subterminal spine on posterior margin of peduncle short, reaching only to level of the proximal part of marginal spine-row of exopod. The spine-row is long, composed of about 30 short spines (fig. 55). Distal to the spine-row there are 2 lateral and 2 terminal spines. Fourth pleopod with posterolateral corner of

peduncle produced and acutely pointed, process in front of exopod base straight and blade-shaped (fig. 57). Fifth pleopod (fig. 58) with ventral process between rami pear-shaped and produced to form acute point. Rami short and comparatively broad (fig. 59) with dense row of short spines on distal half of lateral margin, composed of 7 lateral and 2 distal spines. Sixth pleopod (fig. 60) with process between



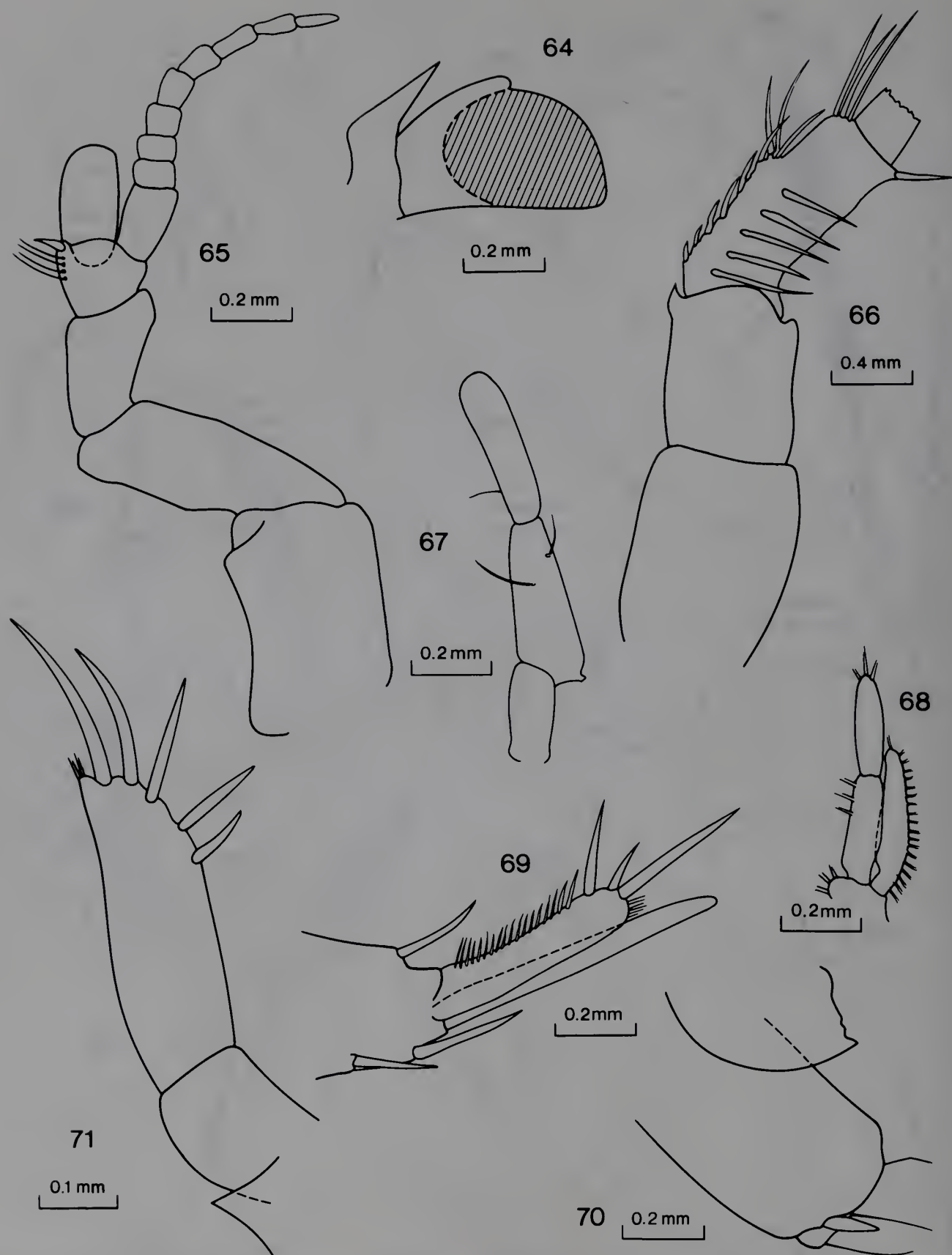
Figs 55—63 *Nebalia antarctica* n. sp., female holotype. 55. Exopod of 1st pleopod. 56. 4th pleon segment epimeron. 57. Proximal part of 4th pleopod. 58. Basis of 5th pleopod. 59. Ramus of 5th pleopod. 60. 6th pleopod. 61. Crenelation on posterior dorsal margin of 7th pleon segment. 62. Anal scale. 63. Telson and furca with detail of armature.

rami acutely pointed, a dense row of lateral and terminal spines covers more than half the lateral margin of ramus, composed of 9 spines.

Type and paratypes in British Museum (Nat. Hist.), London, type no. 1988: 95

FURTHER MATERIAL EXAMINED

1. 'Discovery' Exp. Winter Quarters, Hut Point, D. net, Oct. 1, 1902, 1 specimen.
2. Same locality, No. 6 Hole, 130 fathoms, Feb. 2, 1903. 1 specimen.
3. Same locality without further data. 1 specimen and 2 specimens.



Figs 64—71 *Nebalia falklandensis* n. sp., female holotype. 64. Compound eye. 65. Antennule. 66. Antenna. 67. Mandibular palp. 68. Maxillary palp. 69. 1st pleopod. 70. 4th pleon segment epimeron and proximal part of 4th pleopod. 71. 5th pleopod.

4. 'Terra Nova' st. 331. 1 specimen.

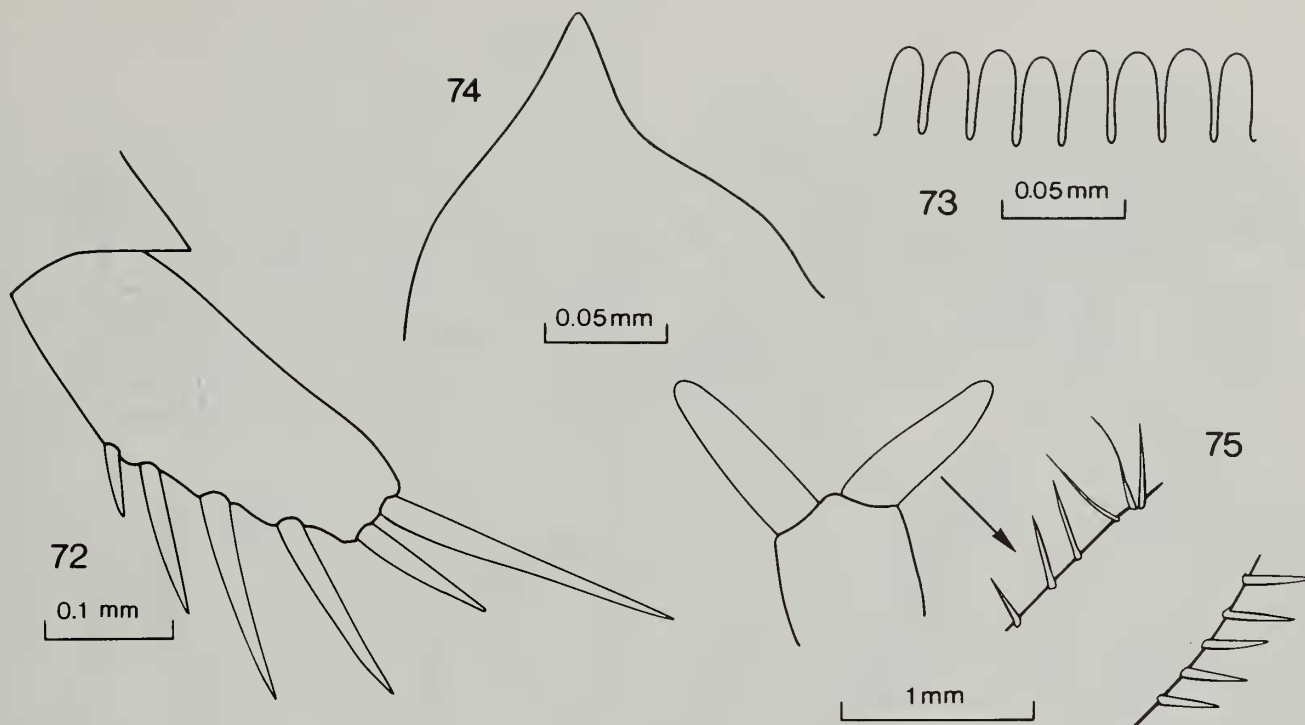
5. King George V Land, Commonwealth Bay, Boat Harbour, 5 fathoms, June 6, 1912 1 specimen.

FURTHER DISTRIBUTION: Antarctic, Wilhelm II Land and Adélie Land.

***Nebalia falklandensis* n. sp.**

Description of female holotype.

TYPE LOCALITY: Falkland Islands, 'Discovery', St. 51, off Eddystone Rock, May 14, 1926, only holotype.



Figs 72–75 *Nebalia falklandensis* n. sp., female holotype. 72. 6th pleopod. 73. Crenulation on posterior dorsal margin of 7th pleon segment. 74. Anal scale. 75. Telson and furca with detail of armature.

Status of female: Prae-ovigerous.

Carapace length: 2.6 mm

Rostrum: removed and measured by Cannon (1931), length/width ratio reported to be 2.07:1.

Pleon, telson, furca: Epimeron of 4th pleon segment with posterolateral corner produced to form a short and not very acute point, posterior margin somewhat irregular, possibly slightly damaged (fig. 70). Crenulation on posterior-dorsal margin of pleon segments 6 and 7 with denticles broadly rounded (fig. 73). Anal scales (fig. 74) short with point somewhat closer to medial margin, 'shoulder' broad and rather distinct. Furca (Fig. 75) with rami short, not much longer than telson and gradually tapering.

Compound eye: (fig. 64) with short eye-stalk, ommatidial part covering nearly 4/5 of its length. Eye papilla distinct but not produced over dorsum of eye. Supraorbital plate covering proximal ommatidia.

Antennule: (fig. 65) with 2nd article of peduncle nearly twice as long as 3rd article, 4th article with only one spine on distal corner. Antennular scale about twice as long as wide, ventral margin nearly straight. Flagellum about half as long as peduncle, with 11 articles.

Antenna: (fig. 66) with 3rd article about 1.5 times as long as 2nd article, lateral spine-row with 5 spines.

Mandibular palp: (fig. 67) with 2nd and 3rd articles subequal, 2nd article with small tubercle on proximal corner and with one short subterminal and one lateral seta; 3rd article hardly expanding distally. Marginal spine-row covering about 4/5 of margin (note position of proximal spine in fig. 67).

Maxilla: (fig. 68) with 1st article of endopod only very slightly longer than 2nd article. Exopod reaching well beyond apex of 1st article.

Thoracopods In order to evade excessive damage to the unique specimen the thoracopods were not dissected.

Pleopods: First pleopod (fig. 69) with peduncle slightly longer than endopod. Subterminal spine on the posterior margin of peduncle short, reaching only to level of proximal part of

spine-row on exopod. This spine-row is rather short and composed of 19 spines only, the distal ones clearly stronger than the others. Distal to the spine-row there are 2 lateral, 1 subterminal, and 1 terminal spine. Fourth pleopod (fig. 70) with posterolateral corner of peduncle truncate. The process in front of the exopod is short and acutely pointed. Fifth pleopod (fig. 71) with the process between rami triangular and acutely pointed. Ramus with distal article 3 times as long as wide, with a row of 3 lateral spines on distal part of margin and 2 somewhat longer terminal spines. Sixth pleopod with process between rami acutely pointed (fig. 72). Ramus not much more than twice as long as wide; 4 spines on distal half of lateral margin and 2 terminal spines.

Type in British Museum (Nat. Hist.). Type no. 1988:97

Nebalia cannoni n. sp.

Description of female holotype.

TYPE LOCALITY: South Georgia, 'Discovery' st. 144, 54°04'—53°38' S, 36°27'—36°26' W, 155–178 m Jan. 5, 1927.

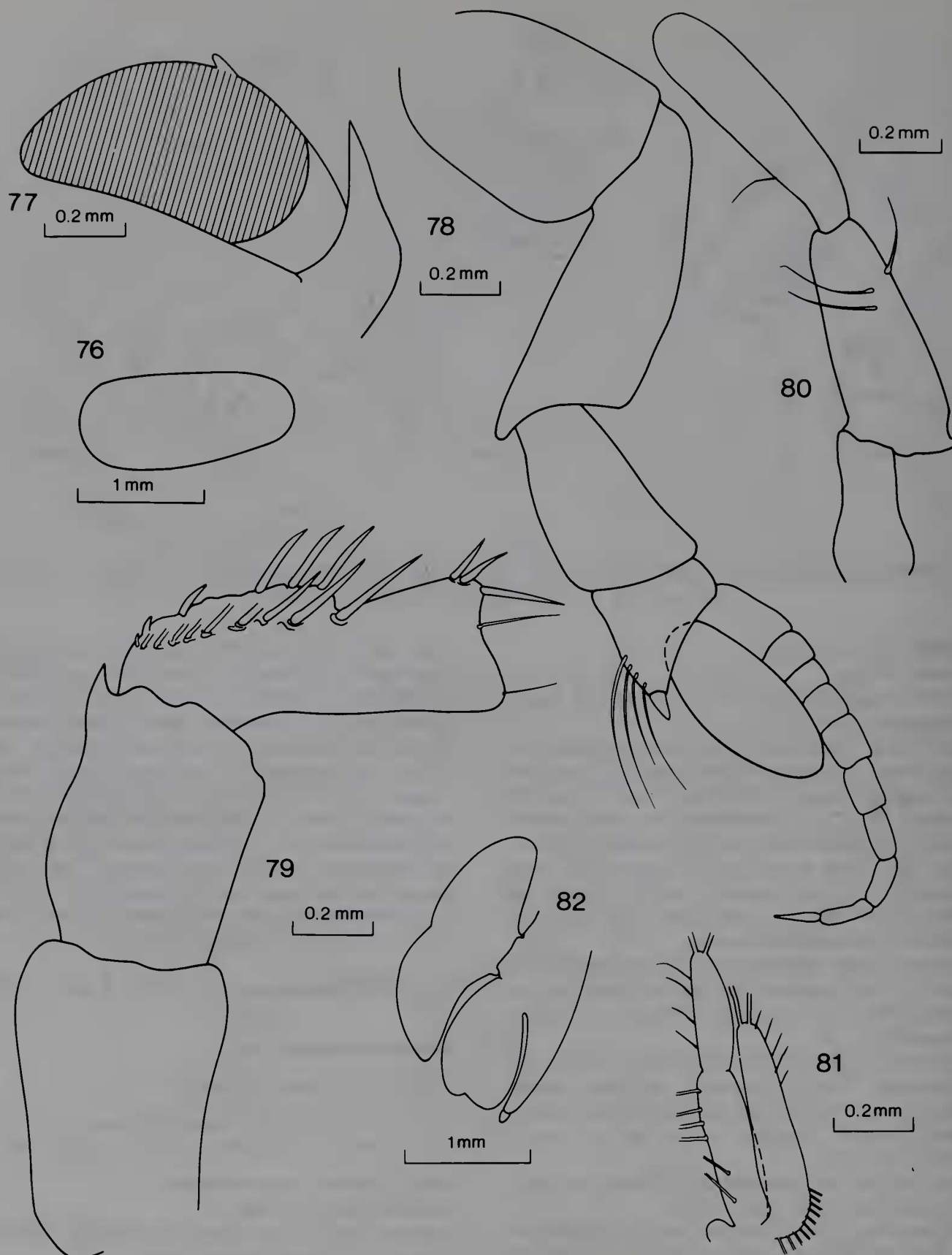
Status of female: Prae-ovigerous.

Carapace length: 5.5 mm.

Rostrum: (fig. 76) with sides nearly parallel, distally tapering abruptly to a broadly rounded apex.

Pleon, telson, furca: Epimeron on 4th pleon segment (fig. 84) with posterolateral corner produced and pointed. Posterior margin denticulate, distal denticles very narrow, the more proximal ones rounded to sub-acute. Denticles on posterior dorsal margin of 6th and 7th pleon segments (fig. 87) not very closely packed, sub-acute. Anal scales (fig. 88) with long, blunt point over medial part of scale, lateral margin sloping nearly evenly without distinct 'shoulder'. Furcal rami (fig. 89) tapering very slightly, subequal to combined length of telson and 7th pleon segment.

Compound eye: (fig. 77) large, with ommatidial part covering



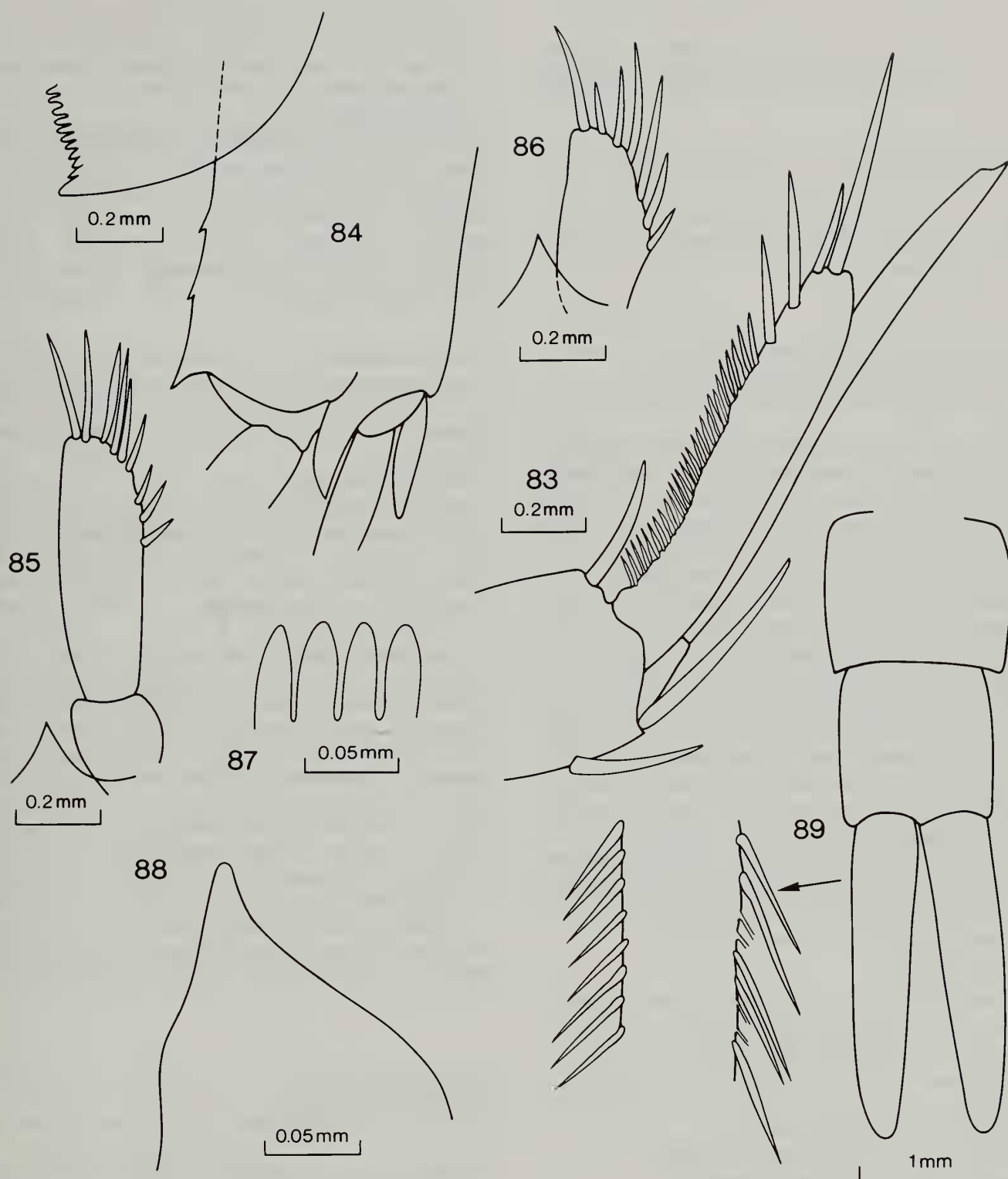
Figs 76–82 *Nebalia cannoni* n. sp., female holotype. 76. Rostrum. 77. Compound eye. 78. Antennule. 79. Antenna. 80. Mandibular palp. 81. Maxillary palp. 82. 3rd thoracopod.

nearly the whole eye-stalk. Eye papilla well developed and projecting freely over dorsum of eye. Supraorbital plate short.

Antennule: (fig. 78) with 2nd article of peduncle about 1.5 times as long as 3rd article, 4th article with only one spine on distal corner. Antennular scale elliptical and about 2.3 times as long as wide. Flagellum much shorter than peduncle, with 10 articles.

Antenna: (fig. 79) with 2nd article of peduncle about 4/5 the length of 3rd article. Lateral spine-row on 3rd article commencing proximally with some setae, gradually replaced by spines distally. Total number of spines and setae 10. Flagellum longer than peduncle.

Mandibular palp: (fig. 80) with 3rd article slightly longer than 2nd article, 2nd article with small tubercle on proximal corner and with one short subterminal seta and 2 lateral setae, 3rd



Figs 83—89 *Nebalia cannoni* n. sp., female holotype. 83. 1st pleopod. 84. 4th pleon segment, epimeron and proximal part of 4th pleopod. 85. 5th pleopod. 86. 6th pleopod. 87. Crenelation on posterior dorsal margin of 7th pleon segment. 88. Anal scale. 89. Telson and furca with detail of armature.

article slightly expanding distally. Marginal spine-row covering 2/3 of lateral edge, position of proximal spine indicated in fig. 30.

Maxilla: (fig. 81). Second article of endopod about 2/3 length of 1st article, exopod reaching nearly to middle of 2nd endopod article.

Thoracopods: (fig. 82). Thoracopods 2–7 with exopod and epipod large. Endopod proportionally short, reaching just past exopod.

Pleopods: First pleopod (fig. 83) with peduncle and endopod

subequal in length. Subterminal spine on peduncle posterior margin not reaching to centre of spine-row on exopod. Exopod proportionally long, spine-row with about 30 spines, distally with 2 lateral and 2 terminal spines. 4th pleopod (fig. 84) with posterolateral corner of peduncle produced to form an acute point, its posterior margin with a few denticles. Fifth pleopod with process between rami short and acutely pointed, 2nd article of rami about 3 times as long as wide, with a row of short spines along distal part of lateral margin, totalling 9 lateral and terminal spines (fig. 85). Sixth pleopod

(fig. 86) with process between rami short and acutely pointed, rami short and nearly triangular, with a row of 7 spines along distal two thirds of lateral margin.

Holotype in British Museum (Nat. Hist.), London, paratypes in Institute of Oceanographic Sciences, Wormley, Godalming, England. Type no. 1988:96.

FURTHER MATERIAL EXAMINED

South Georgia, 'Discovery' St. 45, 2.7 miles S. Jason Light, 238–270 m. April 6, 1926. 1 specimen.

This species is dedicated to the late Professor H. G. Cannon in recognition of his important contributions to the knowledge of the Leptostraca.

DISCUSSION AND CONCLUSIONS

For a long time it has been recognized that the taxonomy of *Nebalia* in the Southern Oceans has been very unsatisfactory (cf. Calman 1917, 1927, Cannon 1931, Johnson 1970). The re-discovery of *N. longicornis* Thomson (see p. 73) has now made this critical revision possible. The inclusion of numerous morphological features not considered by any previous author, except to some extent Barnard (1914), has also contributed materially to the new results presented here.

The long-prevailing unsatisfactory state originated from Thiele's (1904) misidentification of a juvenile nebalid as *N. longicornis*, now known to be a *Sarsinebalia* species. On this conclusion (and also the acceptance of Claus' (1887) wide species concept of leptostracans), Thiele based his comprehensive discussions on the taxonomy of *Nebalia* species and thus created difficulties for later workers. In the revision here at least 10 distinct species are recognized as having previously figured under the name '*N. longicornis*'. Of these it has been possible to identify 4 with sufficient certainty to describe them as new species and also to present a revised list of the southern hemisphere *Nebalia* species as follows:

1. Established species:

- N. longicornis* G.M. Thomson (1879), SE New Zealand
- N. capensis* K.H. Barnard (1914), S. Africa
- N. ilheoensis* Kensley (1976), SW Africa
- N. strausi* Risso (1826), St. Helena, NE Atlantic, W Mediterranean
- N. patagonica* n. sp., Magellan Region
- N. antarctica* n. sp., Antarctic coastal waters
- N. falklandensis* n. sp., Falkland Islands
- N. cannoni* n. sp., S. Georgia

2. Species for which published observations indicate that they are new to science without permitting a description:

- N.* sp., New Britain, Blanche Bay (Thiele 1904)
- N.* sp., Brazil, Ubatuba (Wakabara 1964)
- N.* sp., Singapore, (Johnson 1970)

3. Records without further relevant information:

- N. chilensis* (Claus 1887). *Nomen nudum*, most probably a new species
- N.* sp. Loyalty Islands, Lifu. (Thiele 1904, '*Nebalia longicornis*')

This more realistic species concept of the genus *Nebalia* has materially increased the number of southern hemisphere species but these must represent only a small fraction of *Nebalia* species present in the region. Previous studies on

N. E. Atlantic nebalids (see Dahl, 1985) combined with unpublished observations on collections from N. W. Atlantic, N. E. Pacific and Australian regions, indicate that the numbers of leptostracan species for these respective areas are far fewer and more restricted than, for example, isopods, amphipods, cumaceans and tanaidaceans occurring in comparable habitats.

The Leptostraca and their extinct phyllocarid relatives date back to the Ordovician and have conserved many primitive features. They provide us with a most important source of information concerning early malacostracans. Hopefully the present elucidation of some taxonomic problems will facilitate future critical research on various aspects of leptostracan biology in the Southern Hemisphere.

ACKNOWLEDGEMENTS. The present study was supported by grants from the Swedish Natural Science Research Council and the Royal Physiographic Society, Lund, and by the granting of facilities at the Department of Zoology, University of Lund by Professor Rolf Elofsson.

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I am greatly indebted to Miss Joan Ellis, Crustacea Section, British Museum (Nat. Hist.) for her untiring help and patience, to Dr Michael Thurston and Miss K. G. Chidgey, Inst of Oceanographic Sciences, Godalming for making available 'Discovery' collections, to Professor Torben Wolff, University of Copenhagen for access to the specimen of *Sarsinebalia* which provided the key to the discussions by Thiele (1904, 1905), and to Mr Roy Oleröd, State Museum of Natural History, Stockholm, for the material of *N. patagonica*. Miss Ylwa Andersson and Mrs Gunilla Bergh helped me with many practical problems, and my special thanks are due to Mrs Astrid Ulfstrand for invaluable help in making my drawings ready for publication.

Last but not least my cordial thanks are due to Dr Roger Lincoln for seeing this paper through the press and to Dr R. W. Ingle for highly appreciated criticism and many linguistic improvements.

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